

## 4 Insight, imagination and invention: Tool understanding in a non-tool-using corvid

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### Introduction

The ability of animals to use tools has tended to represent a hallmark of intelligent behavior; i.e., those species that use tools are thought to be smarter than those species that do not. However, many species have been described as tool users, including species that we do not traditionally endow with complex cognition (Beck, 1980). For example, sea otters float with flat rocks on their chests onto which they break shellfish; green herons lower bait or lures (feathers, flowers or insects) onto the surface of the water to attract fish, which they then catch. Tool manufacture, rather than tool use *per se*, may be a finer-grade distinction in terms of intellectual capacity.

Evidence supporting a relationship between tool use and intelligence can be seen in analyses of species of birds and mammals who demonstrate true tool use (i.e., use of objects detached from the environment as tools, such as probes or hammers), have relatively larger brains than species which either do not use tools, or which only demonstrate proto-tool use (i.e., use of objects *in situ* to facilitate the function of an action, such as dropping shells onto a rock to break them; Lefebvre *et al.*, 2002; Reader & Laland, 2002). It not clear whether these are meaningful relationships due to issues with the data used (see below) or the result of some other factor, such as the diet of tool users being better than non-tool users, which has the resultant effect of causing increases in brain size.

But is there any evidence that tool users are actually smarter than non-tool users? In this chapter I will discuss a series of experiments on a member of the corvid family of birds, rooks (*Corvus frugilegus*). Rooks have not been observed using tools in the wild and do not spontaneously use objects as tools in captivity. After examining whether rooks could solve a causal reasoning task that had been adapted for non-tool-using species (two-trap-tube task; Seed *et al.*, 2006), we wanted to further investigate what this species may have understood about how tools worked, what made a functional tool and even whether certain materials could be manipulated to make them into functional tools. This chapter will describe these tasks in detail, but extend the discussion on one remarkable result and its implications for our understanding of insight, imagination and invention.

## Are tool users smarter than non-tool users?

### Tools and brains

Theories as to why the brain, and subsequently intelligence, evolved are still the subject of great debate. Sociality, technology, environmental complexity, extractive foraging, diet, climatic variability and the physical environment have all been proposed as drivers for an increase in brain size and subsequent leaps in intellect during the evolution of primates (Gibson, 1986; Dunbar, 1992; Sterelny, 2003; Potts, 2004), and presumably other animals displaying complex cognition, such as corvids, parrots, elephants and cetaceans (Emery, 2006; van Horik *et al.*, 2011).

The argument is that greater computing power requires a more sophisticated processor, which is reflected in the size of the brain over that required for basic bodily functions, control of movement, etc. This is why *relative brain size* is often used as a proxy for neural processor. This may not necessarily be the most appropriate measure (Healy & Rowe, 2007); indeed, studies in primates have found that overall brain size is a more informative measure when predicting general intelligence (Deaner *et al.*, 2007). Chittka and Niven (2009) even question whether a large brain adds any computational complexity over that seen in much smaller brains, such as in invertebrates. Other problems regarding brains that are often overlooked are that: brains are often not measured correctly using modern stereological techniques; data sets tend to be an accumulation of brain volumes from different sources, that either used different methods to process or measure the brains; and the data sets are usually incomplete (i.e., missing species), which may skew subsequent correlations. In particular, the Stephan data set on primate brains (and brain parts) that is used over and over again is 30 years old; each species is often based on only one individual and not always the same sex for each species; the brains were processed using very old methods and have not been verified to check that they represent the brain areas they are said to demark (Stephan *et al.*, 1981).

The problems in the collection and use of socioecological data are equally as problematic. For example, the data on tool use are based on the frequency of reports in the literature by amateur ornithologists and field primatologists. In the majority of cases, tool use was not the primary purpose of the observation and the frequency of tool use by the individual species (i.e., whether it is habitual or one-off) is not clear. Although collection of data is entirely dependent on research effort, there seems to be little or no effort to control the conditions in which the data were reported. For example, it may be very difficult to report tool use in a nest- or canopy-dwelling species in which clear observations of its behavior are impossible.

These technical issues therefore suggest that studies on brain–behavior relationships may be useful as a first step in determining where to look for cognitive differences, but cannot answer the question of whether tool users are smarter than non-tool users.

## Physical cognition

What about evidence from laboratory tasks? There are three lines of evidence that suggest tool use is not necessarily related to being smarter: (1) species that use tools in the wild which have problems with tool-related physical cognition tasks; (2) species that use tools that perform better on tool-related physical cognition tasks when a tool does not have to be used; and (3) species that do not use tools in the wild which perform well on tool-related physical cognition tasks.

First, tool-using species do not necessarily solve tool-related physical problems. In a series of physical cognition tests, Povinelli (2000) described the difficulties chimpanzees had with tasks testing their understanding of traps, such as trap-tube and trap-table problems. These tasks focus on causal reasoning (i.e., what is the effect of performing some action when there is an obvious obstacle that will prevent an alternative effect, such as pulling food over a hole will cause the food to fall into the trap, whereas pulling the food away from the hole will result in gaining access to it) and an understanding of gravity. Chimpanzees require around 80–100 trials to learn to avoid the trap in simple versions of this task (Limongelli *et al.*, 1995; Povinelli, 2000; however see Mulcahy & Call, 2006), but do not appear to transfer knowledge between different trap problems (Martin-Ordas *et al.*, 2008).

Tool-using New Caledonian crows (NCCs), in some cases, do not fare much better. When given a choice of *Pandanus* leaf tool to use to extract meat from a hole (the tool was already located in the hole) – either oriented with barbs in an upright-position (functional) or with barbs facing downwards or barbs not present (non-functional), many of the crows tested did not chose the functional tool or did not flip the non-functional tool to make it functional (Holzhaider *et al.*, 2008). However, in a similar setup, the crows did flip a non-functional stick tool (with a functional lateral extension poking outside the hole) to become a functional tool, suggesting that perhaps the NCC does not attend to barbs when using this particular tool.

Studies on undergraduate students have revealed surprising inadequacies in their tool-choice behavior. For example, when presented with the rope-and-banana problem – in which they are asked to choose between a series of images of bananas and ropes with differing degrees of connection between the two objects, to pull on a rope to bring a banana toward them – only half of the subjects select the image of the rope tied around the banana. Some subjects choose the image of the rope lying under the banana, whereas other subjects only choose images of the rope that touched the banana, either on top of or next to it (Silva *et al.*, 2008). Silva and Silva (2006) also found that undergraduate students made irrational decisions on trap-table tasks, by not necessarily choosing a tool on the side of the table without a trap (actually only a painted trap) compared to the side with the functional trap.

Second, tool-using species may perform better on tool-related physical tasks when they do not have to use a tool. As stated earlier, chimpanzees do not necessarily display proficient understanding of the trap-tube problem. However, when certain constraints on how tools can be used in the tube are removed, such as increasing the width of the tube, allowing the apes to pull the food toward them rather than push it away, then the chimpanzees' performance improves (Mulcahy & Call, 2006). A perhaps surprising constraint on physical

reasoning is tool use itself. Chimpanzees asked to solve the trap-box problem (like the two-trap-tube problem, see below) were given two versions; one in which they could use a tool to move the food, or a second in which they could move the food directly using their finger. Chimps that used their finger learned the task much faster than chimps that had to use a tool (Seed *et al.*, 2009), suggesting that tool use adds an additional level of cognitive load onto the task, when compared to the task not requiring tool use.

Finally, non-tool-using species may also demonstrate success on tool-related physical tasks. Non-tool-using species have been tested for their comprehension of tool-related physical tasks. For example, when given the choice between different hook-shaped tools or between pieces of cloth with food placed on top or to the side of the cloth, cotton-top tamarins and vervet monkeys made choices based on relevant (e.g., shape) rather than irrelevant (e.g., color) features of the tools (Hauser, 1997; Hauser *et al.*, 1999; Santos *et al.*, 2003, 2006).

Although string pulling in birds may not strictly be classified as tool use (St Amant & Horton, 2008), it does require a complex series of object manipulations akin to tool use. It has been described for a number of non-tool-using birds, such as ravens, keas and African gray parrots, and has even been proposed as evidence for insight (Heinrich, 1995; Pepperberg, 2004; Heinrich & Bugnyar, 2005; Werdenich & Huber, 2006). However, pulling up a string with food attached, although not a natural behavior for birds, is part of most perching birds' behavioral repertoire, as it replicates the actions used in eating (e.g., standing on the food, reaching down and pulling off pieces of the food), and so would not fulfill various criteria for insight (see below).

Finally, non-tool-using rooks have been tested for their understanding of physical concepts, such as contact and causal reasoning, using the expectancy violation procedure (Bird & Emery, 2010) and various trap-problems, such as the two-trap-tube task (Helme *et al.*, 2006; Seed *et al.*, 2006; Tebbich *et al.*, 2007; also see Liedtke *et al.*, 2011 for similar studies in non-tool-using keas, but with a lack of success). For example, rooks look longer, more frequently and with a longer first-look duration at images that are impossible (i.e., violate physical reality, such as an inanimate object floating in mid-air), than images that are possible, such as the same object resting on a flat surface (Bird & Emery, 2010). This method has been used to great success in human babies to test for their implicit understanding of physical concepts like contact; the patterns of the rooks' looking behavior are identical to six-month-old babies.

An adapted version of the trap-tube task (two-trap-tube task; Seed *et al.*, 2006) with two traps, one functional (i.e., traps the food) and one non-functional (i.e., is either baseless so the food falls through or the base has been raised so that food passes over the trap), and an inserted tool to eliminate the need for tool use, has been used to test for causal reasoning, while attempting to eliminate explanations for responses based on perceptual discriminations and associative learning using transfer tests. Seven out of eight rooks tested on the two-trap-tube task learned to avoid the food falling into the functional trap within 40–70 trials and transferred their performance to a different trap configuration within ten trials. One rook was found to transfer immediately (or in one case, by trial 2) when previously rewarded non-functional traps were pitted against one another (such as a trap without a base and a trap with a raised base on the same tube), but with an external manipulation that made one of the non-functional traps functional.

One example was lowering the whole tube, so that the trap without a base was now provided with a base (i.e., the wooden platform it had been lowered onto) and a second example was adding rubber bungs into either end of the tube, but allowing a stick tool to pass through), so that pulling the food toward the previously rewarded raised-base trap would now trap the food (Seed *et al.*, 2006). The performance of tool-using NCC on trap problems, such as the two-trap-tube task (Taylor *et al.*, 2009), is certainly not any better than found in non-tool-using rooks, so this and other evidence presented briefly here does not appear to differentiate tool users from non-tool users (Emery & Clayton, 2009). So what is the extent of a non-tool-using animal's understanding of tools?

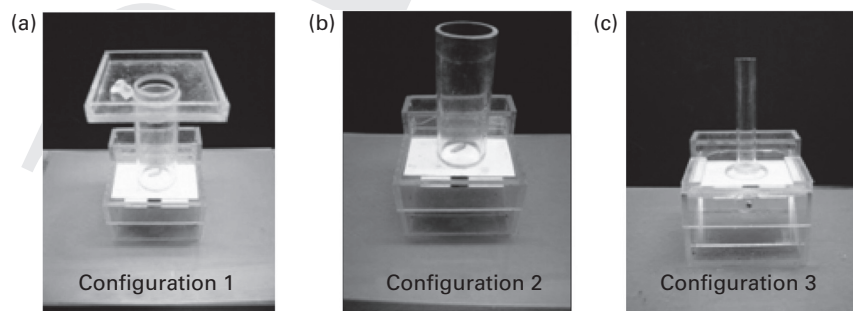
### What does a non-tool-using corvid know about how tools work?

Although rooks have not been observed using tools, either in the wild or in captivity, they do interact with their physical environment, either in terms of building nests or extractive foraging. Rook nests are found at the top or near the top of deciduous trees, and are maintained throughout the lifetime of the pair who originally built the nest. The nests are built using a combination of long sticks, mud, grasses and moss, alongside other natural and artificial materials. Any damage to the nest is repaired. The nests have to withstand extremes in weather conditions, including high winds, rain and snow. Although study of the cognition of nest-building is in its infancy (Healy *et al.*, 2008), we claim that if any species uses cognition to build its nest, then rooks would be a strong candidate.

Additional support for the notion that rooks may understand their physical environment has recently been found regarding their innate knowledge of contact using an adapted expectancy violation paradigm described above (Bird & Emery, 2010).

### Training, transfers and triangulation

In a recent study (Bird & Emery, 2009a), four rooks were trained to use stones as tools in a platform-releasing task (see Figure 4.1). In this task a tasty treat was placed on a



**Figure 4.1** Photographs of the tube platform tasks: (a) original training-tube with a platform located next to the aperture on which a stone was placed (Configuration 1); (b) wide-aperture tube (Configuration 2); and (c) narrow-aperture tube (Configuration 3). Photographs by Chris Bird/Nathan Emery.

collapsible platform under a vertical tube. Dropping an object, such as a stone, into the tube, caused the platform to release the food.

The birds rapidly learned this behavior, first taking only five trials to consistently nudge stones placed at the aperture of the tube to cause the platform to deposit its reward, and eventually picking up stones at the base of the tube or elsewhere in the aviary to put into the tube.

The rooks therefore rapidly learned the affordances of the task: that dropping a stone of a certain shape and size would release the platform. We were not particularly interested in how the rooks learned the original task mechanism (accident [the most likely occurrence], social learning, individual trial-and-error, innovation, ghost controls, etc.), only that they learned how the task worked. We have never claimed that the rooks originally dropped stones into tubes using insight, contrary to some suggestions (von Bayern *et al.*, 2009). Our claim for insight refers to a specific form of tool-related behavior (see below).

Our test that the birds understood the task affordances was to determine if they (1) dropped other objects of equal weight into the tube; (2) refrained from choosing objects that were of an insufficient weight; and (3) that they chose objects that would fit into the tube when the tube aperture was decreased in width, but which would function as appropriate tools.

In all cases the rooks made the correct choice of tool on the first trial that they were presented with the manipulated task. For example, the rooks were initially provided with large stones as tools (and were subsequently rewarded when dropped), but were then given a choice of either the same-sized stones or smaller stones. When the tube aperture was wide (i.e., the original size), the birds predominantly chose the large stones (albeit with some choices of the small stones). When the aperture of the tube was decreased, the birds (after one trial) only chose small stones. In the first trial the birds chose a large stone, tried it, found that it did not fit into the tube; then, on the second and subsequent trials, only chose small stones.

The rooks could also manipulate the stones in order that they could fit into the narrow aperture tube. When presented with either large, round stones or long, thin stones that were the same length as the large stones, but narrow, the birds rotated the stones into the correct orientation in order to fit into the narrow aperture tube. They did this on the first trial and three-quarters of the subjects did this without trying to fit the stone into the tube first.

### Functional tool choice

These results suggest that the rooks appreciated that some stones were functional and others were not, or at least, were not without some form of manipulation. These results also suggest that the birds may have understood the mechanics of the task and responded to changes in these affordances with changes in the aperture of the tube. But how did the rooks respond to changes in the available tools? The rooks were then provided with completely new objects that could be used as tools, such as sticks of various lengths, widths and weights. For example, a light, thin stick would fit into a narrow aperture tube, but would not have sufficient weight to trip the platform, whereas a thick, heavy stick would have sufficient weight, but would not fit into a narrow aperture tube.



The birds performed different actions on the different sticks, depending on the size of the aperture. If the aperture size was wide, and the birds were presented with a heavy stick, they would drop the stick into the tube and collect the worm. If the birds were presented with a long, light stick, they would insert the stick into the tube, but push down onto the stick at the same time, adding the necessary force that would trip the platform without weight alone. If the birds were presented with either a wide, heavy stick or a long, thin stick, they chose the appropriate tool depending on the aperture of the tube (wide stick for wide aperture, long stick for narrow aperture). We do not know what information the rooks may have been using to drive their decision making; however, it is likely that the rooks chose the correct stick (light and thin or heavy and thick) the first time they were presented with them, based on a combination of their visual appearance, size and the shape of the aperture. Their subsequent actions with the sticks (i.e., pushing down on the light stick or dropping the heavy stick) could be achieved through rapid feedback of the weight of the stick, also combined with previous experience and then feedback from the consequences of using the stick for the first time (i.e., that the light stick was not heavy enough to displace the platform). This information could then have driven behavior on subsequent trials.

The rooks were then presented with a choice of a functional tool or a non-functional tool, such as either a functional long stick and a non-functional large stone or a functional small stone and a non-functional short, wide stick, both with a narrow aperture tube. All birds chose the appropriate functional tool during the first trial for the functional stone versus non-functional stick choice, and three out of four of the birds chose correctly on the first trial for the functional stick versus non-functional stone choice (and the fourth bird chose correctly on the second trial).

### Tool modification

What may turn a non-functional object, such as a branch with side twigs and leaves attached, into a functional tool, such as a stick probe, is the ability to modify the object in an efficient manner. This can be the result of removing items from the main object, such as stripping off twigs, or sculpting the object so that it transforms into a different shape, such as molding the end of a broken twig into a hook.

Tool-using capuchins were presented with a tube-problem in which the stick tools they could use to push the food out of the tube needed to be modified in one of three ways. The sticks were presented: in a bundle that was too large to fit into the tube without being dismantled; in three short pieces that needed to be attached together to form a longer stick to reach the food; or as two cross pieces that were attached to the stick which had to be pushed out so that the stick could fit into the tube (Visalberghi & Limongelli, 1996). Capuchins were tested to see whether they could modify the tools to push the food out of the tube, but more importantly, whether they modified the tools before trying to insert them into the tube. If they modified the stick before an attempt, this suggested that they had formed a representation of a functional tool. Although capuchins quickly solved the three tasks, they did not show any improvement over time and made a number of significant errors, whereas chimpanzees and children did not make these errors.

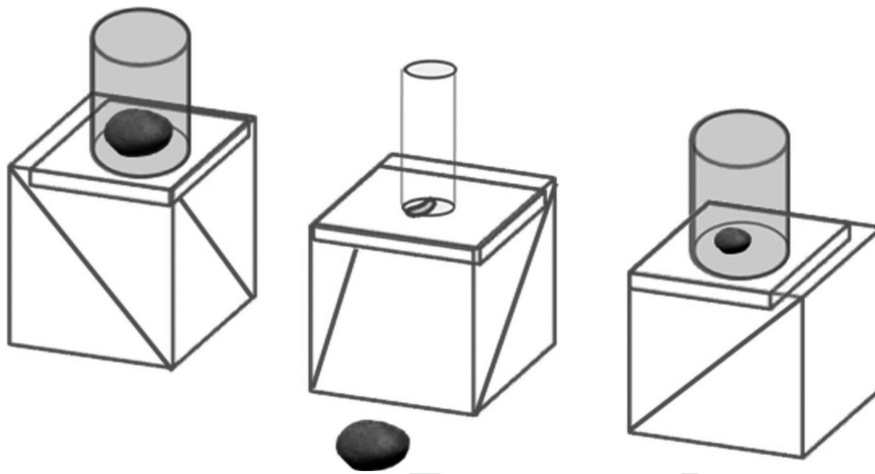
Although rooks do not make tools, we were interested, based on our earlier findings, as to whether rooks would modify natural stick tools with side twigs that could not fit into the tube, by removing the twigs and hence turning the stick into a functional tool. We found that the rooks did not remove the side twigs before inserting the stick into the tube. However, this appeared to be because the side branches were too cumbersome to remove (without hands), and so the birds used leverage from the tube to break off the twigs. It is important to note that the rooks inserted the longest part of the branch into the tube before modification, although this could have been because they were attempting to trigger the platform without modification or to increase stability for modification. Sticks required 1–4 modifications (based on the number of side twigs) and the rooks made 1–7 modifications per stick, which were 100% successful as tools if modified.

### Sequential tool use

Humans (and in some cases, chimpanzees) often use multiple tools to achieve a goal, either using one tool to support, modify or even make another tool (metatool use; Matsuzawa, 1991), or using one tool in order to reach a second tool (sequential tool use). In the animal tool-use literature, these two terms are often used interchangeably in error (unfortunately including by ourselves: Bird & Emery, 2009a). So, metatool use is often used to refer to sequential tool use, in which an animal can use one tool (that is non-functional in terms of accessing the goal object) to reach a second tool (from a choice) that is functional. NCCs have been tested on both two-step (Taylor *et al.*, 2007) and three-step (Wimpenny *et al.*, 2009; Taylor *et al.*, 2010) sequential tool-use problems and have demonstrated great proficiency on this task. The test itself, especially in more complex forms with multiple steps, could be thought of as a planning test equivalent to the classic Tower of Hanoi (or London) task in human psychology (Tower of Hanoi: move a stack of discs largest at the base and smallest at the top from the left peg to the right peg via a middle peg, making sure that the discs finish stacked largest at the base, smallest at the top and do so in the smallest number of moves; Shallice, 1982). But the test does not necessarily have to be solved using goal-directed behavior or planning (as suggested by Wimpenny *et al.*, 2009). Certainly, it is difficult to propose a more complex mechanism than chaining (i.e., reinforcing individual actions in a sequence to form a complex behavior) if only one choice of tool is available or if the initial choice is between one tool that has previously been rewarded and one that has never been rewarded (as in Taylor *et al.*, 2007; see also Clayton, 2007). Other problems with previous tasks raised by Wimpenny *et al.* (2009) were whether the inaccessible tool was located close to the reward and so increasing the chance that the subject would retrieve it by chance or if the complexity of the task was increased in a stepwise fashion, thus increasing the opportunity for learning.

In our study of sequential tool use, we tried to eliminate these problems by providing the rooks with three tubes; two side tubes with wide apertures containing either a large stone on the platform or a small stone and a central tube with a narrow aperture containing a worm (Figure 4.2). The rooks were then presented with a large stone, which they could either insert into the tube containing the large stone, the tube containing





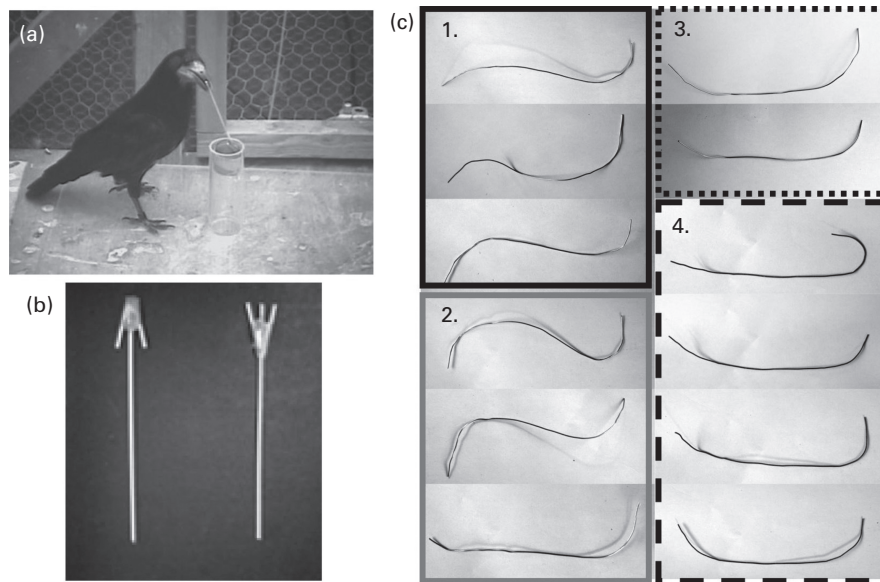
**Figure 4.2** Drawing of the sequential tool-use task (Bird & Emery, 2009a), using three tube platforms; the first tube holds a large stone, the second tube holds a small stone and the middle tube holds a worm. The subject is provided with a large stone. Drawing by Chris Bird.

the small stone or the tube containing the worm. All four subjects spontaneously solved the task on the first trial, inserting the large stone into the tube with the small stone, and then inserted the small stone into the narrow aperture tube to release the worm. Three out of four subjects demonstrated 100% success (mean  $96.7 \pm 2.6\%$  success across all subjects). It is difficult to explain the rooks' success, especially on the first trial, in terms of chaining, trial and error, training or chance retrieval, but we cannot categorically ascribe planning without the addition of control conditions, such as removing the reward to determine whether the stone dropping was goal-directed.

### “Necessity is the mother of invention”

One significant difference between chimpanzees and NCCs is whether they create and/or use hooks; NCCs do, chimpanzees do not. Wild NCCs create hooks from the ends of branches that have been stripped of all side twigs; the broken end is sculpted until it is clean and shaped into a hook (Hunt, 1996; Hunt & Gray, 2004). In addition, a captive female crow (Betty) was given a tube task in which meat was placed into a bucket at the bottom of the tube and then given a hook made from wire. However, when the dominant male (Abel) stole this tool and only a straight piece of wire remained, Betty created hooks by bending the wire (Weir *et al.*, 2002). This remarkable finding has proven difficult to replicate in other individuals, suggesting that Betty may have either done this before when previously kept in captivity, or that she may have been just an exceptional crow.

We therefore gave rooks hook-shaped tools made from wooden sticks with a V-shape taped to the bottom of the stick (Figure 4.3). The hook tool was placed next to a novel task modeled on Weir *et al.* (2002), in which a small card bucket with a handle was placed at the bottom of a vertical tube. A worm was placed inside the bucket. The rooks were very successful in using the hook to pull the bucket out of the tube (mean  $90.8 \pm 4.3\%$  correct),



**Figure 4.3** Photograph of (a) the rook using a pre-made wooden hook tool to retrieve a bucket containing food from a vertical tube; (b) wooden hook-shaped tools (V-shaped and  $\wedge$ -shaped tools); and (c) hook tools produced by the rook subjects. Birds 1 (black border) and 2 (gray border) form one pair; birds 3 (small dash border) and 4 (large dash border) form a second pair. Photographs by Chris Bird/Nathan Emery.

with three out of four birds successful on the first trial and the final bird successful on the second trial. All the birds inserted the hooked end into the tube first, even though they had previously been rewarded for inserting sticks (without hooks) into tubes (see earlier).

We then provided the rooks with a choice of tools: either the V-shaped tool they had previously used or a novel  $\wedge$ -shaped tool (Figure 4.3b). The two tools were similar (i.e., made of sticks and tape), except that the hook end was either functional or non-functional. All subjects inserted the V-shaped end into the tube significantly more than the  $\wedge$ -shaped end, although this may have been due primarily to their previous success with this tool.

Due to the rooks' success with wooden hook tools, we decided to determine whether the non-tool-using rooks would create their own hook tools. We therefore provided the rooks with a straight piece of wire (17 cm long) and the same tube/bucket apparatus for ten trials. *All four rooks modified the wire and successfully retrieved the food.* Three out of four subjects were successful on their first trial and the fourth subject was successful on the fourth trial. It should be noted that birds were only successful in creating hooks on four out of ten ( $n = 2$ ) or three out of ten ( $n = 2$ ) trials. An analysis of the hooks themselves found that successful tools were  $100 \pm 8.5^\circ$  angled, whereas unsuccessful hooks were  $75 \pm 4.5^\circ$  angled. This was in contrast to Betty's hooks, which were all less than  $75^\circ$  angled (Weir *et al.*, 2002). Of particular interest, and something that as yet we cannot explain, the subjects' tools were constructed of two designs, either a curved hook or an S-shaped hook (i.e., a hook at both ends; Figure 4.3) and these designs were conserved within pair bonds, such that pair A favored design A and pair B favored design B. How

this information may have passed between the partners or whether this was just a case of random occurrence is not yet clear.

The fact that the rooks created a tool (hook) from a novel material (wire) on the first trial on which it was presented, when they do not use tools in the wild and with only limited experience of a functionally similar, but not perceptually similar, hook tool, provides a reasonable case for insight (see later for a definition). We discuss this proposal, evidence supporting the proposal and why we think that alternative explanations are not sufficient to explain the behavior, below.

### Aesop's Fable realized

Of the many Aesop's Fables that feature a corvid is the story of "The Crow and the Pitcher." In the fable, a thirsty crow comes across a pitcher of water, but the level of the water is too low for the crow to reach. A number of stones are lying around the base of the pitcher. The crow hits upon the idea of placing the stones into the pitcher until the water level rises enough for it to drink and quench its thirst. This story is frequently used to suggest insight or the moral of the story: "Necessity is the mother on invention."

Tasks based on manipulating water have only recently been attempted with animals. Mendes *et al.* (2007) tested orangutans on an experimental design based on the fable, but instead of water being present in a pitcher, or in their case a vertical tube, the tube was empty except for a peanut. The apes appeared to spontaneously add water to the tube by taking a mouthful from a nearby water source and spitting it into the tube (Mendes *et al.*, 2007). In control conditions, in which the peanut was accessible without adding water to the tube, the orangutans did not collect water, suggesting that their behavior was goal-directed. Mendes *et al.* (2007) suggested that this was evidence for insightful behavior and challenged corvid researchers to test for similar behavior in crows in order to emulate the original fable.

We therefore adapted the original fable (rather than use Mendes *et al.*'s [2007] design, as crows cannot carry water in their mouths like apes), using a vertical tube containing some water, but with a worm floating on the surface (housed in a "boat" to avoid the worm sinking). The birds were presented with this novel task – novel as they had not been presented with a vertical tube containing water previously – and next to the tube were a pile of large stones (a similar size to the stones they had been previously rewarded for dropping into vertical tubes in Bird & Emery, 2009a). The rooks spontaneously dropped the appropriate number of stones into the water to raise the worm to within reach (Bird & Emery, 2009b; Figure 4.4). As the birds had been previously rewarded for dropping stones into tubes, albeit tubes not filled with water or requiring a number of stone drops in succession before receiving a reward, we do not suggest that this behavior is an example of insight (see below). The rooks' behavior is likely based on generalizing from their previous experience and responding to immediate feedback as the worm steadily approached them without moving into reach (although the rooks did not reach for the worm after each stone drop).

In subsequent tests we examined whether the rooks made the most efficient stone choices, i.e., did they choose the larger stones that would result in the greatest displacement



**Figure 4.4** Photograph of a rook placing stones into a vertical tube containing water and a floating worm. Photograph by Chris Bird/Nathan Emery.

of water? Although the rooks spontaneously dropped stones into the tube, when given a choice between large and small stones, they tended to deposit small stones and then eventually (after 5–10 trials) switched preference to large stones. This does not mean that the rooks did not necessarily understand the distinction between the two sizes (Taylor & Gray, 2009), only that both stones had been previously rewarded in earlier tube tasks and both also led to a reward in the Aesop's Fable task. A choice between a functional (i.e., large stone) and non-functional (i.e., polystyrene ball) may have resulted in different responses (see Cheke *et al.*, 2011 for such controls and results in Eurasian jays).

In a final experiment, the rooks were presented with two vertical tubes, one containing sand and the other containing water. Again, surprisingly, the birds preferred to add stones to the tube containing sand, a substrate that could not be displaced. As previously, the birds learned relatively rapidly (5–10 trials) to add stones to the water tube. It is not clear why the rooks initially chose to deposit stones into the sand-filled tube.

### Who's afraid of insight?

Our assertion that wire-bending, at least in rooks, may be an example of insight has met with criticism from many quarters (Kacelnik, 2009; Lind *et al.*, 2009; Shettleworth, 2010; Ed Wasserman & Clive Wynne, reported in Kloc, 2009), often invoking arguments based on an unclear and anthropomorphic definition of insight which is not particularly useful in supporting behavioral criteria that can be tested in non-human animals.

This folk psychological or anthropomorphic concept of insight often refers to the "Aha-moment," in which, after a period of confusion, a solution to a problem appears as if by magic. This is not particularly satisfactory for an empirical approach. Other problems arise when discussing apparent examples of insight by animals. The classic case is the study of chimpanzees by Wolfgang Kohler on the island of Tenerife in the

early part of the twentieth century (Kohler, 1927). In these studies, Kohler provided his apes with various problems in which a tasty treat was out of reach, and the subjects were provided with various objects that could be used in order to either bring the chimp closer to the food or the food closer to the chimp. In one case, a banana was placed inside a cage and the chimp was provided with sticks that could fit together. The chimp eventually combined the sticks into a longer tool that could be used to pull the banana closer. In another case the problem facing the chimps was a banana hanging from a piece of string, too high for them to reach without assistance. After some effort trying to reach the banana without the use of tools and then using individual items, such as standing on a box or reaching with a stick, a chimp eventually moved the box under the banana, stood on the box and reached the banana (more complicated variants included stacking boxes or using a stick to knock the banana onto the floor). Kohler (1927) interpreted the chimp's actions as the result of insight – that the chimp *eventually* visualized the problem as a whole (or *gestalt*) and put the various individual solutions (e.g., stick, box in relation to the banana, etc.) together mentally to form the final solution.

However, this supposed demonstration of insight has been rightly criticized because of the important role of trial-and-error learning and previous experience in forming the chimp's eventual success. Birch (1945), for example, tested young chimps with similar problems and found that the chimps required experience of the individual components of the task in order to demonstrate success.

Even pigeons have been shown to demonstrate behavior resembling insight in a similar problem-solving scenario. Epstein *et al.* (1984) trained a number of pigeons to produce the behavioral components of Kohler's test. Some birds were "trained to push the box towards a green spot .. which was placed at random positions along the base of the chamber wall(s). Pushing was extinguished in the absence of the green spot." The pigeons were then "trained to climb onto the box and peck the banana ... pecking it [the box] was never reinforced" (Epstein *et al.*, 1984: 61). So, both pushing the box and pecking the hanging banana were reinforced. When both banana and box were presented, three pigeons first appeared "confused," looking repeatedly between the box and the banana, which had both been reinforced, but then each subject eventually pushed the box toward the banana until it was directly underneath, then climbed onto the box and pecked the banana. Pigeons that had only been trained on one action (pushing box or pecking banana) did not produce this sequence of actions and hence solve the problem. Epstein *et al.* (1984) suggested that because they had not trained the pigeons to push the box toward the banana (only toward the green spot, which was then extinguished), this could be seen as a case of insight, in the same manner as Kohler's chimps, based on a functional generalization between two previously reinforced actions (push and peck) in relation to two objects (box and banana).

Could this really be a demonstration of insight and could the same behavioral principles explain the rooks' wire-bending? Before attempting to answer this question, it is necessary to evaluate the definition of insight being used here. A clearer description based on behavioral criteria has been provided by Thorpe, who defined insight as "the sudden production of a new adaptive response not arrived at by trial behavior or as the solution of a problem by the sudden adaptive reorganization of experience" (Thorpe, 1964: 110).



The important terms to consider here are *sudden*, *new*, *adaptive* and *reorganization of experience*. For an action to be considered the result of insight, it must be spontaneous (i.e., not the result of explicit training or trial and error), novel (i.e., not performed before), functional (i.e., solve the problem and be goal-directed) and built from previous, untrained, similar behavior (i.e., not produced from copying earlier learned responses, but adapting previous behavior into new actions).

These behavioral criteria can be applied to any action that is proposed as insightful. For example, in the case of using water as a tool by orangutans described earlier (Mendes *et al.*, 2007), we cannot be certain that the behavior was insightful because, although it was spontaneous, functional and built from previous behavior, we do not know whether the behavior itself was novel (i.e., moving water from one container to another via spitting). More information on the previous behavior of the orangutans in this case would provide stronger support for insight using Thorpe's definition; for example, how often do the orangutans spit water during their day-to-day lives outside the context of the experiment?

What about Epstein's pigeons? Their behavior was not spontaneous (it was based on training), not functional (no reward), not novel (pecking and pushing – a form of peck – are both in a pigeon's repertoire) and was not adapted from previous similar behavior (rather than previous same behavior), so could not be considered as insight in any sense.

Finally, what about rooks? Wire-bending was spontaneous (performed on the first trial), novel (wire-bending, hook-making or even tool-making are not within the behavioral repertoire of rooks and not possible outside the context of the experiment, in contrast to the spitting orangutans who have constant access to water), functional (brought the food to within reach) and adapted from previous behavior (using wooden hook tools to raise buckets containing food and inserting sticks into tubes). We are therefore confident that the rooks' actions constitute an unambiguous case of insightful behavior.

We will consider these ideas in detail:

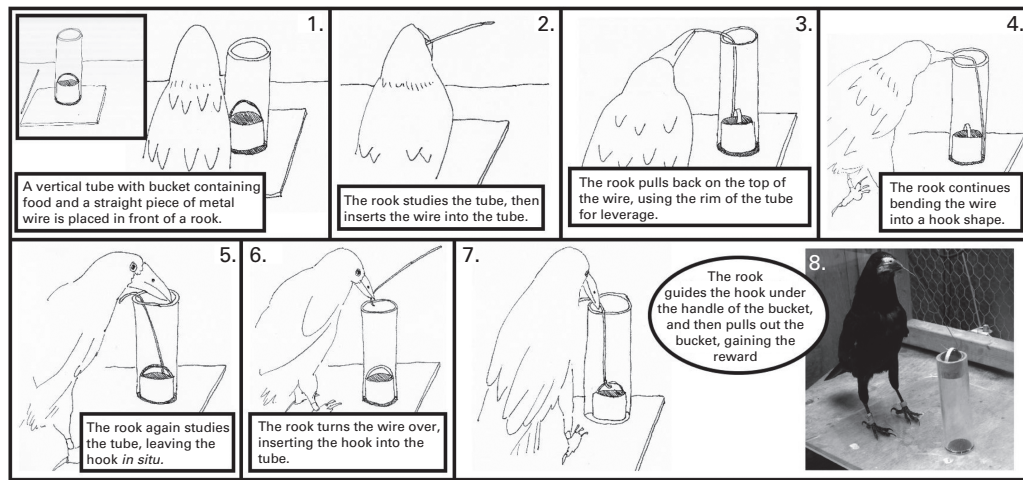
- (1) Rooks do not use tools in the wild or in captivity during their daily lives. When rooks are presented with objects that *can* function as tools, rooks will use them in an appropriate context, such as pulling food up on a piece of string (Seed, Emery & Clayton, unpublished observations), pulling a string with another rook to pull in a wooden shelf holding food (Seed *et al.*, 2008), pulling a stick to drag food out of a clear Perspex tube (Helme *et al.*, 2006; Seed *et al.*, 2006; Tebbich *et al.*, 2007) and inserting sticks/dropping stones into tubes to release a platform or raise water (Bird & Emery, 2009a). However, these are examples of basic tool use, not insight. The action of bending wire is not something that is part of rooks' normal behavioral repertoire. Wire-bending is making a tool from a novel material. Although straight wire could potentially be used as a functional tool, and indeed both rooks (Bird & Emery, 2009a) and NCCs (Weir *et al.*, 2002) were relatively successful in using the straight wire, they were more successful when the wire was bent into a hook.
- (2) Rooks were hand-raised. Their developmental and experimental history was well documented and controlled. We are certain that the rooks had no experience of wire



in an experimental context and the only experience outside of experiments was of the wire that formed their aviaries.

- (3) The rooks had no previous experience of wire hooks. The first time the rooks saw a piece of wire bent into a hook was when they had formed one themselves. The rooks also could not have formed reward associations between wire and food. It is an open question as to why they inserted the wire into the tube, although it is likely that the rooks generalized their previous use (and reinforcement) of sticks; however, this cannot explain how they came to bend the wire into hooks.
- (4) The only experience rooks had of hooks were wooden sticks with a V-shape taped to one end. The rooks were also given some trials with a choice between a functional V-shaped wooden hook and a non-functional  $\wedge$ -shaped wooden hook. These hooks do not look like the wire hooks created by the rooks (see Figure 4.3). It is possible that the rooks formed a mental image of a functional hook tool and then used this template to form a hook from the novel material.
- (5) The rooks' behavior was spontaneous, produced on the first trial in which they experienced the novel material. Therefore, there was no potential for trial-and-error learning.
- (6) The rooks did not appear confused at any time during a trial and we did not observe a change in state from "confusion to solution" (i.e., an "Aha-moment"). In both Epstein *et al.*'s (1984) and Kohler's (1927) studies, at some point during proceedings, the pigeons and chimpanzees appeared to be in a confused state, i.e., they looked frequently between the objects available to them without acting or they repeatedly attempted to reach the banana that was out of reach. The rooks did not do this. They tended to look at the tube from different angles and they did not attempt to reach the food without before inserting and bending the wire.
- (7) The rooks could not have accidentally created a hook. If hook-making was accidental, then surely the rook would have attempted to pierce the worm with the straight piece of wire at the start of every trial, rather than concentrate on manipulating the end of the wire closest to the opening of the tube.
- (8) The finished hook was not located next to the food. Once the hook was created, the rook left the tool *in situ* and examined the task again (Figure 4.5). The rook then removed the tool from the tube, flipped it over, inserted the hooked end into the tube, manipulated the hook until it passed under the handle of the bucket and then pulled the tool upwards until the bucket and reward were removed from the tube (Figure 4.5).

It is very easy to claim that wire-bending in rooks is *just the same* as the pseudo-problem-solving displayed by Epstein's pigeons and just leave it at that. However, they are very different problems, applied in completely different contexts that actually make such simple exertions non-parsimonious and frankly implausible. Hopefully, this attempt to dissect both Epstein's results with pigeons and Bird and Emery's results with rooks provides some structure on which to make reasoned arguments about insight (as a form of mental operation) rather than dissenters crying anthropomorphism and associative learning without any scientific structure to their criticisms.



**Figure 4.5** Diagram redrawn from the original video displaying a typical successful wire-bending trial. (1) The rook retrieves the wire (a novel material) – this behavior has not been previously reinforced. (2) The rook studies the tube without pecking at the worm and then inserts the wire into the tube – insertion of sticks has been previously reinforced, albeit with wooden sticks. (3–4) The rook bends the wire using the top of the tube – this behavior has never been previously reinforced and is not part of the rooks' behavioral phenotype (i.e., rooks are not tool users). (5) The rook studies the worm/bucket, but again does not peck at it – behavior is not reinforced. (6) The rook removes the hooked end of the wire and turns it over so the hooked end is now in the tube near the bucket – perceives that the functional end is not in a functional position, so removes the wire (behavior is not reinforced) and re-inserts (remove and reinsert have never been reinforced, but insertions have been previously reinforced). (7) The rook guides the hooked end under the bucket handle and pulls up the bucket until it is out of the tube – this behavior has been previously reinforced with wooden sticks. (8) Photograph of a rook using a recently created hook tool to pull a bucket out of a tube. Drawings by Nathan Emery. Photograph by Chris Bird/Nathan Emery.

## The how and why of insight in rooks

If we assume that our analysis is correct – that some part of rooks' actions toward certain tools is representative of insight – then why rooks and how could this psychological process be manifest in the rook brain?

There are a number of potential reasons for why rooks. First, although rooks have not been demonstrated to use or make tools in the wild, field studies on rook behavior have not specifically addressed this issue, so it is possible that tool use has just never been reported, but it is present. This seems very unlikely, as rooks are one of the most common European and Asian birds. Amateur and professional birdwatchers have dedicated thousands of hours of observation to this species and fervently submit short notes to ornithological journals reporting unusual behaviors, including potential examples of tool use.

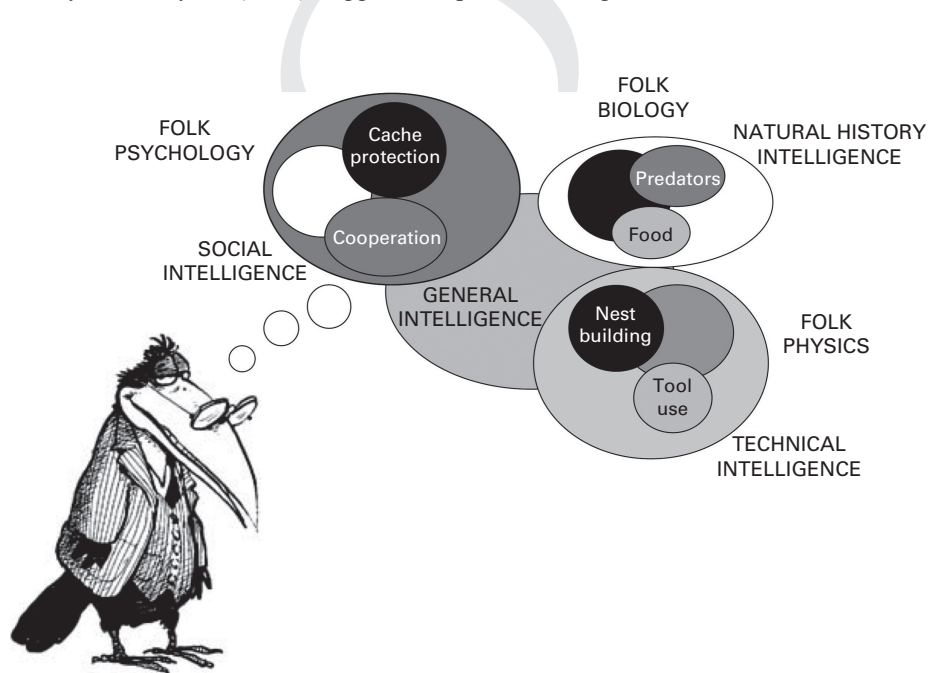
Second, insight and other aspects of physical cognition (folk physics) are the result of non-tool-related behaviors which involved object manipulation, such as extractive foraging. The best candidate is perhaps nest-building (Healy *et al.*, 2008; Walsh *et al.*, 2010), which

requires individuals to form artificial structures from large numbers of objects, such as sticks, mosses and grasses, that can withstand huge fluctuations in temperature, wind, and weather elements, as well as predators, with the function of protecting offspring. Rook nests, in particular, are built at the top of deciduous trees and so are more exposed than most nests. Rooks pairs return to the same nest site each breeding season and repair their nests.

Is there something special about rook nests? For example, do rooks build “better” nests than other birds? How are their nests built, maintained and repaired? Does nest structure improve over time? How is “folk physics” involved in nest construction? Answers to these questions from detailed observations of nest-building behavior, simulations of nests under various climatic scenarios and psychological tests on the possible mechanisms of construction behavior should help answer these questions.

Third, the common ancestor of the *Corvus* genus (or perhaps all corvids) had already evolved technical intelligence and so the behaviors described in this chapter are more common than we perhaps realize. These behaviors may have evolved in response to increased opportunities for object manipulation and extractive foraging in the *Corvus* (or corvid) common ancestor.

Fourth, the rook mind is constructed from a series of adaptive specializations (domain-specific modules) and general processes (domain-general; Figure 4.6). Emery and Clayton (2004) suggested a potential “cognitive toolkit” in corvids and



**Figure 4.6** Diagram representing domain-general and domain-specific (physical, social and natural history intelligence) cognitive architecture in rooks. The domain-specific modules specialize in solving specific socioecological problems using problem-specific processing (e.g., face recognition is important for social cognition), but they also overlap because they also use domain-general processes, such as memory, concepts, causal and analogical reasoning, planning and imagination. The degree of overlap is perhaps more pronounced in *Homo sapiens*.

apes that could be utilized across domains, comprising imagination, prospection, causal reasoning and flexibility. We suggest that as rooks do not use tools in the wild, and yet appear to understand how tools work when tested in captivity, this could be evidence that the cognition underlying their response to tools is domain-general (i.e., independent of the ecological context) and not domain-specific (i.e., dependent on the ecological context). Hence, the rook mind has refined its cognitive architecture from solving one set of physical problems (e.g., nest building) to solving another set of physical problems outside the domain for which it originally evolved (e.g., tool use). Such cognitive architecture may require such general processes as causal reasoning and insight.

How might such a system be realized in the rook brain? Potential models of the cognitive architecture of insight could be based on the associative-cybernetic model (de Wit & Dickinson, 2009) or global workspace theory (Shanahan & Baars, 2005). Both models include a means for simulating alternative actions and scenarios (mental trial and error) without having to act on the simulations, something akin to imagination or insight. The development of such models in terms of insight and imagination *per se* would be a significant step in our understanding of invention and the creative process, but at present such models in this context are unrealized.

## Conclusion

When interpreting an animal's behavior in cognitive terms, especially when those terms have been borrowed from human psychology (or worse, human folk psychology), a cautious approach is essential (Shettleworth, 2010). However, many critics are possibly too quick to dismiss much of animal behavior as “simple” associative learning without considering the animal's behavior in its entirety. Associative learning is anything but simple, and should not be contrasted directly with cognition as if they were polar opposites. Behavior is the result of a collection of different psychological processes working together: perception, learning and cognition. Without discussing or testing the different contributions and forms that these processes take, the “killjoy” hypotheses become as worthless as the “anthropomorphic” terms they are suggested to replace.

In the case of insight described here, Epstein *et al.*'s (1984) studies on pigeons are important, perhaps overlooked, contributions to comparative psychology, but they have tended to be wielded without careful consideration of what arguments they are being used to support. Hopefully, the analysis of the wire-bending study of Bird and Emery (2009a) presented in this chapter may dispel some erroneous notions that the rooks' behavior is a rather simple case of previous experience and conditioning (Lind *et al.*, 2009). By using a clear definition of insight (Thorpe, 1964), we can hopefully distinguish between real candidates for insightful behavior rather than based on our folk psychological notions of insight as the “Aha-moment” (see Chapter 1 for an up-to-date discussion of modern psychological theories of insight). This may as well be a magical process and certainly one that cannot be analyzed at any behavioral level. In getting us closer to the most parsimonious explanation for the processes underlying a particular behavior, we may

advocate a liberal dose of Occam's aftershave (Emery & Clayton, 2008) after the brutal wielding of the razorblade of "killjoy explanations."

## Acknowledgments

The experiments described in this chapter formed part of Chris Bird's PhD thesis. I thank him profusely for his sterling efforts in increasing our understanding of the rook mind. I would also like to thank the three editors, Crickette Sanz, Josep Call and Christophe Boesch, for initially inviting me to the meeting and for their patience in waiting for this chapter to finally appear. I would also like to thank the other meeting participants for a stimulating and enjoyable conference. My research was funded by the Royal Society, BBSRC and University of Cambridge and I was supported by a Royal Society University Research Fellowship.

## References

- Beck, B. (1980). *Animal Tool Behavior: The Use and Manufacture of Tools by Animals*. New York: Garland.
- Birch, H. G. (1945). The relation of previous experience to insightful problem-solving. *Journal of Comparative Psychology*, **38**, 367–383.
- Bird, C. D. & Emery, N. J. (2009a). Insightful problem solving and creative tool modification by captive nontool-using rooks. *Proceedings of the National Academy of Sciences USA*, **106**, 10370–10375.
- Bird, C. D. & Emery, N. J. (2009b). Rooks use stones to raise the water level to reach a floating worm. *Current Biology*, **19**, 1410–1414.
- Bird, C. D. & Emery, N. J. (2010). Rooks perceive support relations similar to six-month old babies. *Proceedings of the Royal Society of London B*, **277**, 147–151.
- Cheke, L. G., Bird, C. D. & Clayton, N. S. (2011). Tool use and instrumental learning in the Eurasian jay (*Garrulus glandarius*). *Animal Cognition*, **14**, 441–455.
- Chittka, L. & Niven, J. (2009). Are bigger brains better? *Current Biology*, **19**, R995–R1008.
- Clayton, N. S. (2007). Animal cognition: crows spontaneously solve a metatool task. *Current Biology*, **17**, R894–R895.
- de Wit, S. & Dickinson, A. (2009). Associative theories of goal-directed behaviour: a case for animal–human translational models. *Psychological Research*, **73**, 463–476.
- Deaner, R. O., Isler, K., Burkart, J. M. & van Schaik, C. P. (2007). Overall brain size, and not encephalization quotient, best predicts cognitive ability across non-human primates. *Brain, Behavior & Evolution*, **70**, 115–124.
- Dunbar, R. I. M. (1992). Neocortex size as a constraint on group size in primates. *Journal of Human Evolution*, **20**, 469–493.
- Emery, N. J. (2006). Cognitive ornithology: the evolution of avian intelligence. *Philosophical Transactions of the Royal Society of London B*, **361**, 23–43.
- Emery, N. J. & Clayton, N. S. (2004). The mentality of crows: convergent evolution of intelligence in corvids and apes. *Science*, **306**, 1903–1907.
- Emery, N. J. & Clayton, N. S. (2008). Imaginative scrub-jays, causal rooks and a liberal application of Occam's aftershave. *Behavioural and Brain Sciences*, **31**, 134–135.

- Emery, N. J. & Clayton, N. S. (2009). Tool use and physical cognition in birds and mammals. *Current Opinion in Neurobiology*, **19**, 27–33.
- Epstein, R., Kirschnit, C. E., Lanza, R. P. & Rubin, L. C. (1984). “Insight” in the pigeon: antecedents and determinants of an intelligent performance. *Nature*, **308**, 61–62.
- Gibson, K. R. (1986). Cognition, brain size and the extraction of embedded food resources. In J. G. Else & P. C. Lee (eds.) *Primate Ontogeny, Cognition and Social Behaviour* (pp. 93–105). Cambridge: Cambridge University Press.
- Hauser, M. D. (1997). Artifactual kinds and functional design features: what a primate understands without language. *Cognition*, **64**, 285–308.
- Hauser, M. D., Kralik, J. & Botto-Mahan, C. (1999). Problem solving and functional design features: experiments in cotton-top tamarins. *Animal Behaviour*, **57**, 565–582.
- Healy, S. D. & Rowe, C. (2007). A critique of comparative studies of brain size. *Proceedings of the Royal Society of London B*, **274**, 453–464.
- Healy, S., Walsh, P. T. & Hansell, M. (2008). Nest building by birds. *Current Biology*, **18**, R271–R273.
- Heinrich, B. (1995). An experimental investigation of insight in common ravens (*Corvus corax*). *Auk*, **112**, 994–1003.
- Heinrich, B. & Bugnyar, T. (2005). Testing problem-solving in ravens: string-pulling to reach food. *Ethology*, **111**, 962–976.
- Helme, A. E., Clayton, N. S. & Emery, N. J. (2006). What do rooks (*Corvus frugilegus*) understand about physical contact? *Journal of Comparative Psychology*, **120**, 288–293.
- Holzhaider, J. C., Hunt, G. R., Cambell, V. M. & Gray, R. D. (2008). Do wild New Caledonian crows (*Corvus moneduloides*) attend to the functional properties of their tools? *Animal Cognition*, **11**, 243–254.
- Hunt, G. R. (1996). Manufacture and use of hook-tools by New Caledonian crows. *Nature*, **379**, 249–251.
- Hunt, G. R. & Gray, R. D. (2004). The crafting of hook tools by wild New Caledonian crows. *Proceedings of the Royal Society of London: Biology Letters*, **271**, 88–90.
- Kacelnik, A. (2009). Tools for thought or thought for tools? *Proceedings of the National Academy of Sciences USA*, **106**, 10071–10072.
- Kloc, J. (2009). Invoking the magic of the mind. *Seed Magazine*. [http://seedmagazine.com/content/article/invoking\\_the\\_magic\\_of\\_the\\_mind/](http://seedmagazine.com/content/article/invoking_the_magic_of_the_mind/).
- Kohler, W. (1927). *The Mentality of Apes*. New York: Vintage Books.
- Lefebvre, L., Nicolakakis, N. & Boire, D. (2002). Tools and brains in birds. *Behaviour*, **139**, 939–973.
- Liedtke, J., Werdenich, D., Gajdon, G. K., Huber, L. & Wanker, R. (2011). Big brains are not enough: performance of three parrot species in the trap-tube paradigm. *Animal Cognition*, **14**, 143–149.
- Limongelli, L., Visalberghi, E. & Boyzen, S. T. (1995). The comprehension of cause–effect relations in a tool-using task by chimpanzees (*Pan troglodytes*). *Journal of Comparative Psychology*, **109**, 18–26.
- Lind, J., Ghirlanda, S. & Enquist, M. (2009). Insight and learning. *Proceedings of the National Academy of Sciences USA*, **106**, E76.
- Martin-Ordas, G., Call, J. & Colmenares, F. (2008). Tubes, tables and traps: great apes solve two functional equivalent trap tasks but show no evidence of transfer across tasks. *Animal Cognition*, **11**, 423–430.
- Matsuzawa, T. (1991). Nesting cups and meta-tools in chimpanzees. *Behavioural & Brain Sciences*, **14**, 570–571.



- Mendes, N., Hanus, D. & Call, J. (2007). Raising the level: orangutans use water as a tool. *Biology Letters*, **3**, 453–455.
- Mulcahy, N. J. & Call, J. (2006). How great apes perform on a modified trap-tube task. *Animal Cognition*, **9**, 193–199.
- Pepperberg, I. M. (2004). “Insightful” string-pulling in grey parrots (*Psittacus erithacus*) is affected by vocal competence. *Animal Cognition*, **7**, 263–266.
- Potts, R. (2004). Paleoenvironmental basis of cognitive evolution in great apes. *American Journal of Primatology*, **62**, 209–228.
- Povinelli, D. J. (2000). *Folk Physics for Apes*. New York: Oxford University Press.
- Reader, S. M. & Laland, K. N. (2002). Social intelligence, innovation and enhanced brain size in primates. *Proceedings of the National Academy of Sciences USA*, **99**, 4436–4441.
- Santos, L. R., Miller, C. T. & Hauser, M. D. (2003). Representing tools: how two non-human primate species distinguish between the functionally relevant and irrelevant features of a tool. *Animal Cognition*, **6**, 269–281.
- Santos, L. R., Pearson, H. M., Spaepen, G. M., Tsao, F. & Hauser, M. D. (2006). Probing the limits of tool competence: experiments with two non-tool-using species (*Cercopithecus aethiops* and *Saguinus oedipus*). *Animal Cognition*, **9**, 94–109.
- Seed, A. M., Tebbich, S., Emery, N. J. & Clayton, N. S. (2006). Investigating physical cognition in rooks. *Current Biology*, **16**, 697–701.
- Seed, A. M., Clayton, N. S. & Emery, N. J. (2008). Cooperative problem solving in rooks (*Corvus frugilegus*). *Proceedings of the Royal Society of London B*, **275**, 1421–1429.
- Seed, A. M., Call, J., Emery, N. J. & Clayton, N. S. (2009). Chimpanzees solve the trap problem when the confound of tool-use is removed. *Journal of Experimental Psychology: Animal Behavior Processes*, **35**, 23–34.
- Shallice, T. (1982). Specific impairments of planning. *Philosophical Transactions of the Royal Society of London B*, **298**, 199–209.
- Shanahan, M. P. & Baars, B. J. (2005). Applying global workspace theory to the frame problem. *Cognition*, **98**, 157–176.
- Shettleworth, S. J. (2010). Clever animals and killjoy explanations in comparative psychology. *Trends in Cognitive Sciences*, **14**, 477–481.
- Silva, F. J. & Silva, K. M. (2006). Humans’ folk physics is not enough to explain variations in their tool-using behaviour. *Psychonomic Bulletin and Review*, **13**, 689–693.
- Silva, F. J., Silva, K. M., Cover, K. R., Leslie, A. L. & Rubalcaba, M. A. (2008). Humans’ folk physics is sensitive to physical connection and contact between a tool and reward. *Behavioural Processes*, **77**, 327–333.
- St Amant, R. & Horton, T. E. (2008). Revisiting the definition of animal tool use. *Animal Behaviour*, **75**, 1199–1208.
- Stephan, H., Frahm, H. & Baron, G. (1981). New and revised data on volumes of brain structures in insectivores and primates. *Folia Primatologia*, **35**, 1–29.
- Sterelny, K. (2003). *Thought in a Hostile World*. New York: Blackwell.
- Taylor, A. H. & Gray, R. D. (2009). Animal cognition: Aesop’s fable flies from fiction to fact. *Current Biology*, **19**, R731–R732.
- Taylor, A. H., Hunt, G. R., Holzhaider, J. C. & Gray, R. D. (2007). Spontaneous metatool use in New Caledonian crows. *Current Biology*, **17**, 1504–1507.
- Taylor, A. H., Hunt, G. R., Medina, F. S. & Gray, R. D. (2009). Do New Caledonian crows solve physical problems through causal reasoning? *Proceedings of the Royal Society of London B*, **276**, 247–254.

- Taylor, A. H., Elliffe, D., Hunt, G. R. & Gray, R. D. (2010). Complex cognition and behavioural innovation in New Caledonian crows. *Proceedings of the Royal Society B*, **277**, 2637–2643.
- Tebich, S., Seed, A. M., Emery, N. J. & Clayton, N. S. (2007). Non tool-using rooks (*Corvus frugilegus*) solve the trap tube task. *Animal Cognition*, **10**, 225–231.
- Thorpe, W. H. (1964). *Learning and Instinct in Animals*. London: Methuen & Co. Ltd.
- van Horik, J., Clayton, N. S. & Emery, N. J. (2011). Convergent evolution of cognition in corvids, apes and other animals. In J. Vonk & T. Shackelford (eds.) *The Oxford Handbook of Comparative Evolutionary Psychology* (pp. 80–101). New York: Oxford University Press.
- Visalberghi, E. & Limongelli, L. (1996). Acting and understanding: tool use revisited through the minds of capuchin monkeys. In A. E. Russon, K. A. Bard & S. T. Parker (eds.) *Reaching Into Thought: The Minds of the Great Apes* (pp. 57–79). Cambridge: Cambridge University Press.
- von Bayern, A. M. P., Heathcote, R. J. P., Rutz, C. & Kacelnik, A. (2009). The role of experience in problem solving and innovative tool use in crows. *Current Biology*, **19**, 1965–1968.
- Walsh, P. T., Hansell, M., Borello, W. D. & Healy, S. D. (2010). Repeatability of nest morphology in African weaver birds. *Biology Letters*, **6**, 149–151.
- Weir, A. A. S., Chappell, J. & Kacelnik, A. (2002). Shaping of hooks in New Caledonian crows. *Science*, **297**, 981.
- Werdenich, D. & Huber, L. (2006). A case of quick problem-solving in birds: string pulling in keas, *Nestor notabilis*. *Animal Behaviour*, **71**, 855–863.
- Wimpenny, J. H., Weir, A. A. S., Clayton, L., Rutz, C. & Kacelnik, A. (2009). Cognitive processes associated with sequential tool use in New Caledonian crows. *PLoS ONE*, **4**, e6471.